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DEVELOPMENT

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JULY 10, 1906

EVIDENCE BEARING ON TOOTH-CUSP
DEVELOPMENT.¹

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IN connection with the work of cataloguing the portion of the Marsh collection of Mesozoic mammals, obtained under the auspices of the U. S. Geological Survey and now deposited in the United States National Museum, I have made some discoveries of seeming importance in the form of evidence bearing on the question of tooth-cusp homologies in the mammalian molars. This evidence I wish briefly to present in the following pages, hoping it may throw some added light on the very important subject of tooth morphology.

Before proceeding, I wish to express my indebtedness to Dr. George P. Merrill for making possible the arrangements for this detailed study of material and for his encouragement in the work; to Prof. Charles Schuchert, of Yale University, for submitting to my hand the type material of the Marsh collection at New Haven; and to Prof. Henry F. Osborn of the American Museum of Natural History, for his courtesy in placing the collection of Mesozoic mammals in that institution at my disposal. My thanks are also due Mr. G. S. Miller, Jr., for his valuable aid in selecting study material from the collection of modern mammals in the National Museum and for a clear translation of Herluf Winge's paper on tooth-cusp development.

¹Based on a study of the Mesozoic Mammal Collection in the U. S. National Museum.

Of the several theories thus far advanced for the evolution of the teeth, none has been entirely satisfactory, and there is still a wide disagreement among authorities, especially as regards the position of the primary cone or "protocone" in the upper molars. As proposed by the late Prof. E. D. Cope and supported by Prof. Henry F. Osborn, the primary cone is to be found invariably on the inner or lingual side of the trigonodont upper teeth, and is the homologue of the central cone in *Triconodon*, in which the three main cusps are arranged in an antero-posterior line, the trigonodont molar having been derived from this form through the shifting of the two lateral cones to the outside. The central cone (*protocone*) remaining on the inner side, thus forms a triangle (*trigon*) with the apex pointing inward. In the meantime, according to this theory, the cusps of the lower molars are supposed to have moved in the opposite direction, leaving the central cusps (*protoconid*) on the outside, forming an oppositely directed triangle (*trigonid*). Thus the primary cones of the upper and lower molars in shifting have completely reversed their positions in relation to each other, the primary cone of the upper molars not only moving to the inner side of the crown, but taking a position in the series inside the primary cone of the lower molars as well.

This theory, so skillfully worked out by Osborn, has been widely accepted as satisfactorily explaining the problem of tooth-cusp evolution. But recent paleontological and embryological investigations have thrown a large amount of discredit on the whole theory. As stated by Wortman, Scott has shown most conclusively, from paleontological evidence, that in the upper molariform premolars the primary cone is on the *outer* side and the subsequently added cusps have a very different history from that proposed by the tritubercular theory for the true molars. The embryological researches of Woodward, Tacker, and others have not only confirmed Scott's theory for the premolars, but show also that in all groups of mammals investigated the antero-external cusp or paracone is first to appear in the permanent upper molars and milk molars, as it does in the premolars, and the order of appearance of the other principal cusps is practically the same as proposed by Scott for the premolars.

Woodward¹ found that in *Centetes* and *Ericulus* the main internal cusp, usually termed the protocone, was first to develop, but he believed this cusp to be the paracone, the whole tooth representing only the antero-external triangle of such a form as *Talpa*, the protocone and metacone not having been developed. This, as stated by Woodward, is a modification of Mivart's view published in 1868,² in which he states his belief that in *Centetes*, *Chrysocloris*³ and like forms, the main portion of the crown represents the union of the two external prisms of *Talpa* and like forms. According to Mivart, the main internal cusp of *Centetes*, *Ericulus*, *Chrysocloris*, etc., was derived by the fusion of the paracone and metacone, while the protocone and hypocone are wanting or rapidly diminishing in size and importance. According to both Woodward and Mivart, therefore, in these forms, which have been considered typical trituberculates, the outer cusps are developments of the cingulum, while the main internal cusp has been wrongly termed the protocone and is in reality the paracone, according to Woodward, or combined paracone and metacone, according to Mivart, while the inner cusp (protocone) is greatly diminished in size or has entirely disappeared. These two authorities, therefore, are agreed on the two points of principal importance regarding *Centetes* and *Ericulus*, viz: (1) the location of the paracone in the main internal cusp and (2) the ultimate loss of the protocone. I strongly concur in these views, for in a series of upper molars, including *Potamogale*, *Solenodon*, *Centetes*, *Ericulus*, *Hemicentetes* and *Chrysocloris* (see figs. 1-6, pl. IV), the stages suggesting the gradual diminishing and final disappearance of the protocone are very complete, amounting almost to demonstration, and there can be little doubt that the molars of the *Centetes* and *Chrysocloris* type have been derived from forms similar to that of *Potamogale*, involving the loss of the protocone. In consequence of this the paracone, or combined paracone and metacone, comes to be the principal inner cusp. In *Potamogale* the

¹ Proc. Zool. Soc. London 1896, 588-589.

² Journ. Anatomy and Physiol., Vol. II, 139, 1868.

³ The form figured by Mivart has since been removed to a distinct genus, *Bematiscus* Cope, Am. Nat., XXVI, 1892, 127. The typical *Chrysocloris* upper molar has no trace of a protocone.

protocone is quite prominent and still typical in form, while in *Solenodon* it is much reduced and is beginning to divide transversely, or more probably is beginning to separate from a likewise reducing hypocone. This is in favor of the view held by Mivart that the simple inner cusp in *Potamogale* and like forms is in reality the fused protocone and hypocone. The reduction is carried still further in *Centetes*, in which two inner cingulum-like cusps appear, one on each side of the enlarged paracone. In *Chrysocloris* and *Hemicentetes* the inner cusp (protocone and hypocone) has entirely disappeared.

Regarding Mivart's "fusion theory," I am inclined to believe that Woodward has not given due weight to the evidence cited by Mivart and that there is considerable support for this theory to be found in the modern bats and insectivores. Mivart considered the *Potamogale* molar as an intermediate form between molars of the *Talpa* type, having two external triangular prisms, and those of *Centetes* and *Ericulus*, having only one such prism. He pointed out that in *Potamogale* there is "a very interesting approximation of the triangular prisms," in which the paracone and metacone, although still remaining distinct, are in very close juxtaposition. This view is strongly supported by a series of bat molars to which Mr. G. S. Miller has kindly called my attention. In this series, which includes *Vespertilio*, *Scotophilus* and *Harpiocephalus*, are suggested the successive steps from *Talpa* to *Potamogale* in the insectivore group. *Vespertilio* represents the normal or more generalized form, in which the protocone is large, the paracone and metacone are widely separated, and the external styles are nearly equal in size. The mesostyle is much reduced in *Scotophilus* and is drawn inward, the paracone and metacone are more closely appressed and the protocone is somewhat shortened. In *Harpiocephalus*¹ the mesostyle has disappeared, the parastyle and

¹The skull of *Harpiocephalus* from which this description was taken was obtained by Mr. G. S. Miller through the kindness of Oldfield Thomas, of the British Museum.

Unfortunately it came too late to be photographed and figured uniformly with the series. Its place is taken on Plate III, by an outline drawing from a figure for Wilhelm Peters' *Fledermäuse des Berliner Museums für Naturkunde* (a projected monograph of the bats).

metastyle have drawn closer together and compose the entire outer portion of the crown, while the paracone and metacone are closely approximated, forming the greater part of the inner portion of the crown, the protocone being very much reduced. Thus in *Harpiocephalus* a stage is reached nearly analogous to that of *Potamogale*, the principal difference being that the metacone is the dominant cusp instead of the paracone, as in the latter genus.¹

From these comparisons it seems reasonably clear that such forms as *Centetes*, *Ericulus* and *Chrysochloris* have attained a secondary or pseudo-tritubercular form by passing through some such stages of evolution as are suggested by the two series here selected. Other examples of a fusing paracone and metacone and reducing protocone may be found in the molars of some of the creodonts and carnivorous marsupials and in the sectorials of many of the carnivores.

From the foregoing it now seems to be demonstrated beyond question that the main inner cone of *Centetes* and *Ericulus* is not the protocone as observed in normal groups, but, if not entirely made up of the primary cusp (paracone), it at least involves that element and Woodward's contention that the evidence of embryology is in entire harmony for the molars and premolars is not controverted by these seeming exceptions as supposed by Osborn.

Wortman of late has strongly opposed what he terms the "cusp migration theory," and has brought considerable evidence to show that, in the creodonts and carnivores, at least, the cusps of the upper molars in general are homologous to those of the molariform premolars and have had substantially the same history in their development.

Against this combined evidence Osborn² has recently reaffirmed the tritubercular theory, "as originally proposed," resting the whole question on the point of evidence as to "whether the main reptilian cone, or protocone, of the ances-

¹ In the Laramie mammals I find that the metacone equals or is larger than the paracone in those forms in which the postero-external heel is well developed in the upper molars.

² Amer. Journ. Science (4), Vol. 17, 1904, 321-323.

tors of the mammals was found upon the antero-internal side or on the antero-external side of the upper molars." This evidence, according to Osborn, is in favor of the tritubercular hypothesis, and conclusive evidence of the theory is furnished in the Jurassic mammal molars. However, a study of all the mesozoic mammal material available has led the present writer to exactly opposite conclusions.

Unfortunately, Osborn's observations were confined to a very limited amount of material, and from a careful examination of the teeth of *Triconodon* and *Dryolestes*,¹ two forms especially studied by him, it seems that his conclusions were based on evident, though perfectly excusable, errors of observation, due doubtless to the minuteness of the teeth and their dark color, which make it difficult in many cases to distinguish, between a fracture and the natural surface of the tooth. Thus, according to Osborn,² the upper molars of *Dryolestes* are "broadly transverse or triangular and upon the *internal* side of each is a large, conical, pointed cusp, *pr*, supported by a large stout fang, . . . The external portion of the crown is depressed, and bears one large antero-external cusp ? *pa* and one smaller postero-external cusp ? *me* which is either partially worn away or less pronounced in development." But there are two important cusps not noted by Osborn, one an external cusp placed anterior to the main external cusp, the other a small but well-defined intermediate cusp appearing on the posterior transverse ridge. Thus there are five distinct cusps instead of three, as stated by Osborn, and these do not form a trigon in the sense that this term has been used, for the main external cusp is in the middle of the base of the triangle instead of forming one of its angles.

In the upper molars of *Triconodon* the three principal cusps are arranged in a direct line, and are nearly equal in size and form, and the two lateral cones are each supplemented by a small but well-defined internal basal heel-like cusp and an external basal cingulum. The main cusps are flattened externally into a continuous wall in one species (see Pl. V, fig. 1), while they are

¹The specimens studied by the present writer and referred to these genera are from the *Atlantasaurus* beds of Wyoming. These beds are usually referred to the upper Jurassic, although they may be lower Cretaceous.

²Amer. Journ. Science (4), Vol. 17, 1904, 322.

much rounded and deeply divided on the inner or lingual side. Thus, there is not the slightest suggestion of a tendency toward an outward movement of the lateral pair of cusps, while it is easily conceivable that the continued development of the two inner heel cusps and outer cingula would early result in a general form of tooth very different in pattern from the tritubercular type which might form the basis for such molars as those of the diprotodont marsupials and many of the rodents or even of the manatee and mastodon. I do not wish to be understood here as implying any relationship between these very diverse forms, but as especially emphasizing the fact that in *Triconodon* is suggested an easy and not improbable way in which some complex molars may have been derived without having passed through the typical tritubercular stage.

Thus, it is shown by this restudy of the two forms, which according to Osborn represent successive stages in the evolution of the mammalian molar, that the gap between them, which was already great, even according to Osborn's interpretation, is very greatly increased especially from the tritubercular theory standpoint. Moreover there is no evidence, in the way of intermediate forms, indicating that *Dryolestes* ever passed through a stage strictly analogous to that of *Triconodon* or that the main internal cusp is in any way homologous to the central cone in the *Triconodon* molars. Furthermore, a critical comparison of these two forms shows that such an hypothesis is beset by many difficulties. The following are the principal ones: (1) The molars of *Triconodon* are larger and fewer in number than in *Dryolestes* indicating a generally higher specialization. (2) The lateral cones in *Triconodon* are already comparatively much specialized, being supplemented by growths of the cingulum externally and heel cusps internally and thus do not especially resemble, either in form or proportions, any two of the external cusps in *Dryolestes*. (3) The external portion of the upper molar in *Dryolestes* (see Pl. V, figs. 2 and 3) is composed of three simple connate cusps supported by two fangs, their general appearance suggesting an arrangement homologous to the three cusps and two fangs of *Triconodon*; while (4) the internal portion of the tooth is a high antero-posteriorly com-

pressed V-shaped cusp supported by a single fang, centrally placed, and exposed on its inner side for the greater part of its length, the maxillary bone apparently not yet having formed a completed socket, or alveolus, for its reception. Thus the whole construction of the inner cusp, which is highly suggestive of a heel development, differs materially from the central cone of *Triconodon*.

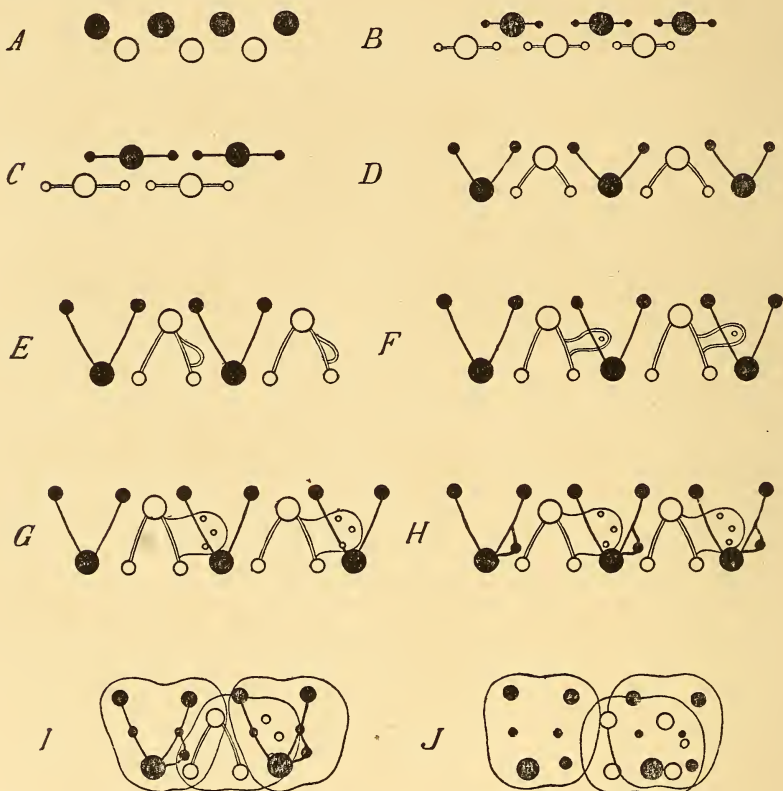


FIG. 11. *Phyletic History of the Cusps of the Ungulate Molars.* A, Reptilian Stage, Haplodont, Permian. B, Protodont Stage (*Dromotherium*), Triassic. C, Triconodont Stage (*Amphilestes*). D, Tritubercular Stage (*Spalacotherium*). E, Tritubercular-tuberculo Sectorial, Lower Jurassic. F, The same, in Upper Jurassic. G, The same, in Upper Cretaceous. H, The same, Puerco, Lower Eocene. I, Sextitubercular-sextitubercular, Puerco. J, Sextitubercular-quadrutubercular, Wahsatch. (After Osborn.)

Considering the outer portion of the *Dryolestes* molar as homologous to the three cones and two fangs of *Triconodon*,

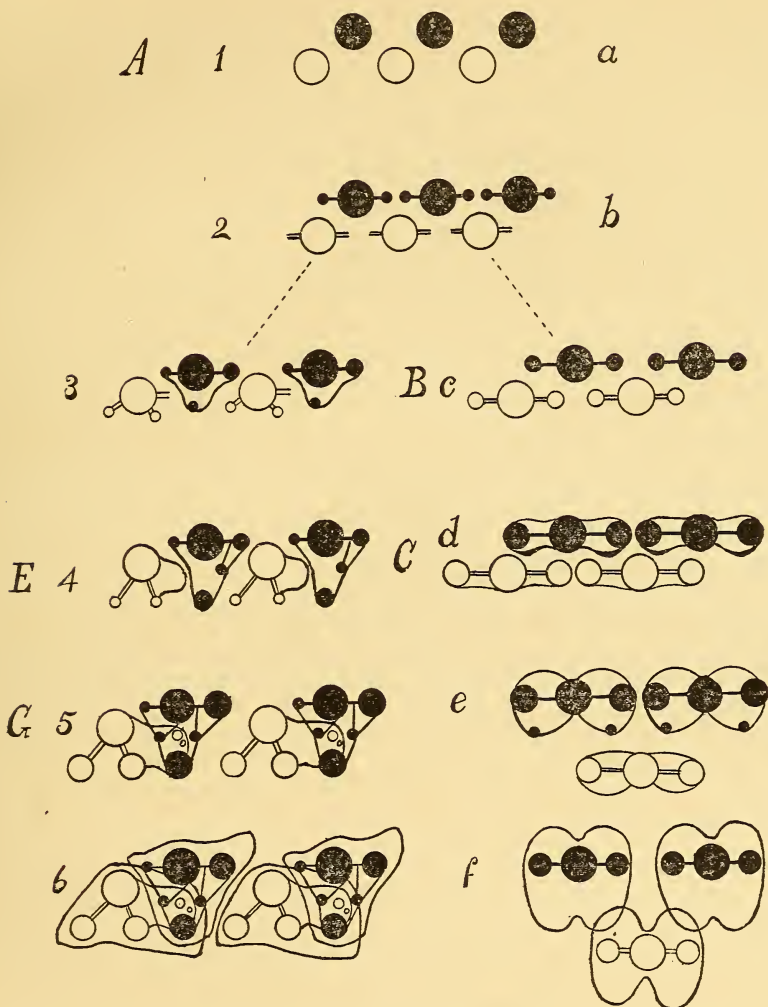


FIG. 12. *Suggested Phyletic History of Two Types of Complex Molars.* [As in Osborn's diagram, the solid black dots represent the cusps of the upper molars, the circles, those of the lower molars.] 1 to 6, Phyletic history of the "Tritubercular" type; a to d, Phyletic history of the "Triconodont" type; e, f, From the brachyodont Triconodont stage to the bilobed hypsodont type of molar.

A, B, C, E and G compare with A, B, C, E and G in Osborn's diagram, fig. 11; 4, *Dryolestes* type, Atlantosaurus beds (? Upper Jurassic); 5 and 6, *Protolambda* or *Pedimys* type, Laramie beds (Upper Cretaceous); d, *Triconodon* type, Atlantosaurus beds (? Upper Jurassic); f, *Palæolagus* type, White River beds (Oligocene).

the derivation of this type of tooth is much simplified, it being not so far removed from the primitive reptilian condition, and though diverging on different lines, is no more specialized, as a whole, than the *Triconodon* type of tooth, the differentiation being carried on more rapidly in the latter in the special development of the anterior and posterior lateral cones and their accessory cusps, while in *Dryolestes* the specialization has apparently been centralized in the development of the high, narrow, heel-like cusp and its supporting fang on the inner side of the molar.

This view is strongly supported by the evidence obtained from still another characteristic Atlantosaurus-beds type of molar represented by *Dicrocynodon*. In this form, Pl. V, fig. 4, the same primitive arrangement of three cusps and two fangs is preserved in the outer portion of the tooth, while on the internal side a large secondary cusp has been developed differing widely in character from that of *Dryolestes*. This cusp is a laterally compressed cone supported by *two* rudimentary fangs and is joined to the outer portion of the tooth by a high, wedge-shaped ridge. The base of the inner cone is greatly expanded anteroposteriorly, curving gently outward toward the external portion of the tooth. Thus the crown, as a whole, is greatly constricted medially with the inner and outer portions superficially resembling each other.

From these observations two important conclusions may be drawn: First, that, leaving out of consideration the multituberculates, there are among the mammals of the Atlantosaurus beds at least three distinct forms of upper molars representing three primitive types of about equal specialization apparently leading off in entirely independent lines. Probably only one of these, *Dryolestes*, represents an ancestral type from which the Upper Cretaceous and later forms possessing trigonodont molars may have been derived. Second, that the evidence derived from the Atlantosaurus beds mammals entirely supports the evidence of embryology and agrees in general with the "pre-molar analogy" theory. Thus, the evidence from all sources points overwhelmingly to the conclusion that the primary cone is to be found on the *outer* side in the upper molars of primi-

tive trituberculate forms and in all forms derived from a tritubercular type of tooth as well, except where the main inner cone (protocone) has been reduced secondarily. The opposite view held by the tritubercular theory now apparently stands on very insufficient evidence, and the proposition that the protocone, of Osborn, represents the primary cusp is entirely without support.

The lower molars of the *Atlantosaurus* beds mammals furnish abundant additional evidence along the line of conclusions regarding the shifting of three cusps from a straight line to form the primitive triangle. In such forms as *Dryolestes* and *Paurodon* we have trituberculate molars in the primitive or forming stage, and, what is most significant, the cusps resemble very closely, both in position and relative proportions, those of the premolars of later types in their early stages of transition to the molariform pattern. In the lower molars of *Paurodon* the crown consists of a high, pointed cusp (protoconid), centrally placed, a low posterior heel, a small antero-internal cusp (paraconid), and a very small median internal cusp (metaconid). The last two form the base of the trigonid. In *Dryolestes* both the trigonid and the primitive heel are somewhat more advanced in development. In still other forms, such as *Manacodon* and *Tinodon*, the two internal cusps are relatively large and the trigonid is fully developed, while the heel, or talonid, is very small or entirely wanting. In all the paraconid and metaconid are entirely on the internal side of the crown, and in these and all the material examined there is not the slightest evidence of any shifting of the cusps, but they seem to have arisen in the positions they now occupy.¹ In *Paurodon* the heel is apparently as much or more developed than either of the internal cusps and seems to have made its appearance even in advance of the metaconid. Also the metaconid is still very rudimentary and is just budding off near the base of the protoconid, but little posterior to its apex and midway of the entire length of the crown, while the place of origin assigned to it by the tritubercular hypothesis is already occupied by the comparatively large heel.

¹ This is in accord with the general conclusions on tooth cusp development reached by Herluf Winge as early as 1882. *Widinsk Meddelelser fn den naturhist. Florence* é Kjobenhavn, 1882, p. 18.

From these observations it seems apparent that the trigonid of the lower molars is not the reverse of the trigon of the upper molars, as held by advocates of the tritubercular theory, and the homologues of the elements of the upper and lower molars, as proposed by this theory, are far from being apparent. (This also accords with the conclusions of Winge.)

The lower molars of *Triconodon* differ from any of the forms just described. They are composed of three nearly equal cone-like cusps arranged like those in the upper molars of this genus in an antero-posterior line. There is no cusp corresponding with the metaconid in *Dryolestes*. There is a continuous basal cingulum on the inner face of the crown, and the posterior cusp is in no way homologous, except in position, to the heel in the lower molars of *Paurodon* and *Dryolestes*.

The mammals from the upper Cretaceous Laramie beds show a great advance in development. The molars of the trituberculate forms of this horizon have passed into a second well-defined stage of specialization which, though varying greatly in detail in the various types, conforms in general to a distinctive pattern which may readily have been derived from some *Atlantosaurus*-beds form, such as *Dryolestes*. An upper molar of *Pedionomys* Marsh, a typical example of the Laramie tritubercular molar, compared with the corresponding tooth of *Dryolestes*, presents the following differences and indicates the principal lines of progression:

(1) The main internal cusp (*protocone*) is much broadened antero-posteriorly; (2) a second small V-shaped intermediate cusp (*protoconule*) has been added; (3) the postero-external cusp (*metacone*) has greatly increased, nearly equaling, both in size and importance, the median external, or primary, cone (*paracone*), while the antero-external cusp (*parastyle*) has remained small and undeveloped. A correspondingly progressive development marks the trigonid and heel of the lower molars.

Thus, the "trigonodont" tooth, or a type of molar with three principal cusps of almost equal importance, arranged in the form of a triangle, makes its first appearance in the Laramie. This pattern of tooth Cope early recognized as a general primi-

tive type, and on its representatives in the lower Eocene he founded the tritubercular theory. That this type is primitive and many, at least, of the later forms have been derived from it, have been too conclusively demonstrated by Cope, Osborn, Scott and others to be seriously questioned; but this early trigonodont form, as is now evident, was derived in a totally different way from that assumed by the tritubercular hypothesis.

An especially interesting feature in these Laramie forms is the oft-repeated appearance in the upper molars of a backwardly extended outer heel-like cusp connected by an elevated ridge with the postero-external cusp. This portion of the tooth is thus converted into a more or less perfect sectorial, or cutting, blade, against which the anterior blade of the trigonid shears, while the greatly broadened heel or talonid of the lower molar, extending backward under the antero-posteriorly expanded protocone of the upper molar, forms a successful crushing apparatus. Thus, so early as the Cretaceous the prevailing molar types were about equally equipped for use as cutting or crushing mechanisms. The creodonts and carnivorous marsupials seem to have early taken advantage of the sectorial blade to the neglect of the crushing heel which gradually diminished in relative size and importance, while in many other forms, using the crushing portion of the tooth most, the sectorial blade was early lost.

Another special character marking the advance of the upper Cretaceous mammal molars is the first indication in a few forms of the postero-internal cusp (*hypocone*), which forms the fourth main cusp in the later quadra-tubercular type of molars. This cusp has apparently been derived, according to the evidence of these Laramie types, from independent sources in different groups of mammals. In a form which Marsh has referred to *Telacodon* a strong cone-shaped cusp has developed on the postero-internal cingulum of the tooth indicating the derivation of the hypocone from that source. Another form, apparently representing an undescribed genus (Pl. V, fig. 7) is evidently developing a hypocone from the primitive posterior intermediate cusp. Still another form, represented by *Proto-*

lambda Osborn, seems to indicate a third source from which the hypocone may have developed. In *Protolambda* the internal heel (protocone) is broadly expanded and flattened posteriorly without a cingulum, yet the peculiar shelf-like form of this portion of the tooth suggests the origin of a hypocone budding off from the protocone independently of either the cingulum or posterior intermediate cusp.

From such a form as that presented in Pl. V, fig. 7, it is but a short step to the typical selenodont artiodactyl type of molar through the progressive development of the V-shaped posterior intermediate cusp. The addition of a second posterior cusp budding off from the enlarged postero-intermediate cusp would readily convert the tooth into a perissodactyl type of molar. Thus is suggested a fourth possible source of origin for the hypocone. This does not necessarily imply an actual relationship of this particular form to the ungulates, but indicates a type closely resembling them which differs widely from the primitive carnivores and insectivores, in which the hypocone, when present, was undoubtedly derived from the cingulum. These observations suggest especially that apparently homologous elements in the teeth of the more highly complex forms may often arise from different sources.

The correlation and homologies of the cusps of the lower molars in comparison with those of the upper series have, for the most part, been left out of this discussion. One observation, in this connection, however, of seeming great importance and significance should be noted here.

In examining a large number of examples of both living and extinct forms, I have found the following associations between the heel of the lower molars and the protocone of the upper teeth to hold constantly true, viz: A functional, broad, crushing protocone is invariably associated with a well-developed crushing heel in the opposing lower molar. A reduced or vestigial protocone is invariably associated with a correspondingly reduced or vestigial heel in the opposing lower molar. Since the heel of the lower molars is admittedly of secondary origin, this feature alone would seem to argue strongly for a like secondary origin for the protocone in the upper molars.

SUMMARY AND CONCLUSIONS.

Summing up the evidence derived from this preliminary study, the following conclusions are suggested:

1. That the evidence obtained from the Mesozoic mammal teeth furnishes no support to the tritubercular theory in so far as it involves the position of the protocone and the derivation of the trigonodont tooth from the triconodont stage through the shifting of the lateral cones outward in the upper molars and inward in the lower molars.

2. That it supports entirely the embryological evidence that the primary cone is the main antero-external cusp, or *paracone*, having retained its position on the *outside* in most upper molars (see exceptions above, p. 95).

3. That it agrees in the main with Huxley's "premolar-analogy" theory, as supported by Scott.

4. That the molars of the Multituberculates, *Triconodon*, *Dryolestes* and *Dicrocynodon*, were apparently derived independently from the simple reptilian cone; hence the supposition follows that the trituberculate type represents but one of several ways in which the complex molars of different groups may have been derived.¹

5. That in the forms derived from the trituberculate type of molar the order of succession of the cusps is not the same in all groups, and apparently homologous elements are sometimes developed from different sources. Hence it follows that *no theory involving an absolute uniformity of succession in the development of complex molars will hold true for all groups of mammals.*

In the foregoing pages I have restricted the use of Osborn's tooth-cusp nomenclature for the reason that, in this particular discussion, there are some cases in which it is not strictly applicable and might lead to confusion.

On similar grounds Dr. Wortman² has expressed the opinion that all attempts to establish a tooth-cusp nomenclature founded on supposed homologies are "foredoomed to failure" and should be entirely abandoned as "useless and confusing." I

¹ Somewhat similar conclusions have been reached from different reasoning by E. S. Goodrich, M. Tims and others.

² Amer. Journ. Science (4), Vol. 16, 1903, 265-368.

agree with the general sentiment expressed (*op. cit.*, p. 366) that, owing to the adoption of different plans in different groups of mammals for increasing the complexity of their molars, no terminology founded on the basis of cusp homologies can be made strictly applicable to all the mammalia. I do not, however, consider this sufficient ground for abandoning absolutely so convenient a system of nomenclature as that proposed by Osborn. Granting that many of the terms proposed are founded on mistaken homologies, it does not necessarily follow that they need be in the least confusing, as suggested by Wortman. For in any system used, in order to make that system of greatest convenience and highest utility, the names once adopted should be permanent and not subject to transfer or substitution on any ground of changed conceptions of homologies or history, for the same reason that generic and specific names are retained regardless of the fact that they may have been given to denote some supposed affinity or characteristic which may later have proved entirely erroneous.

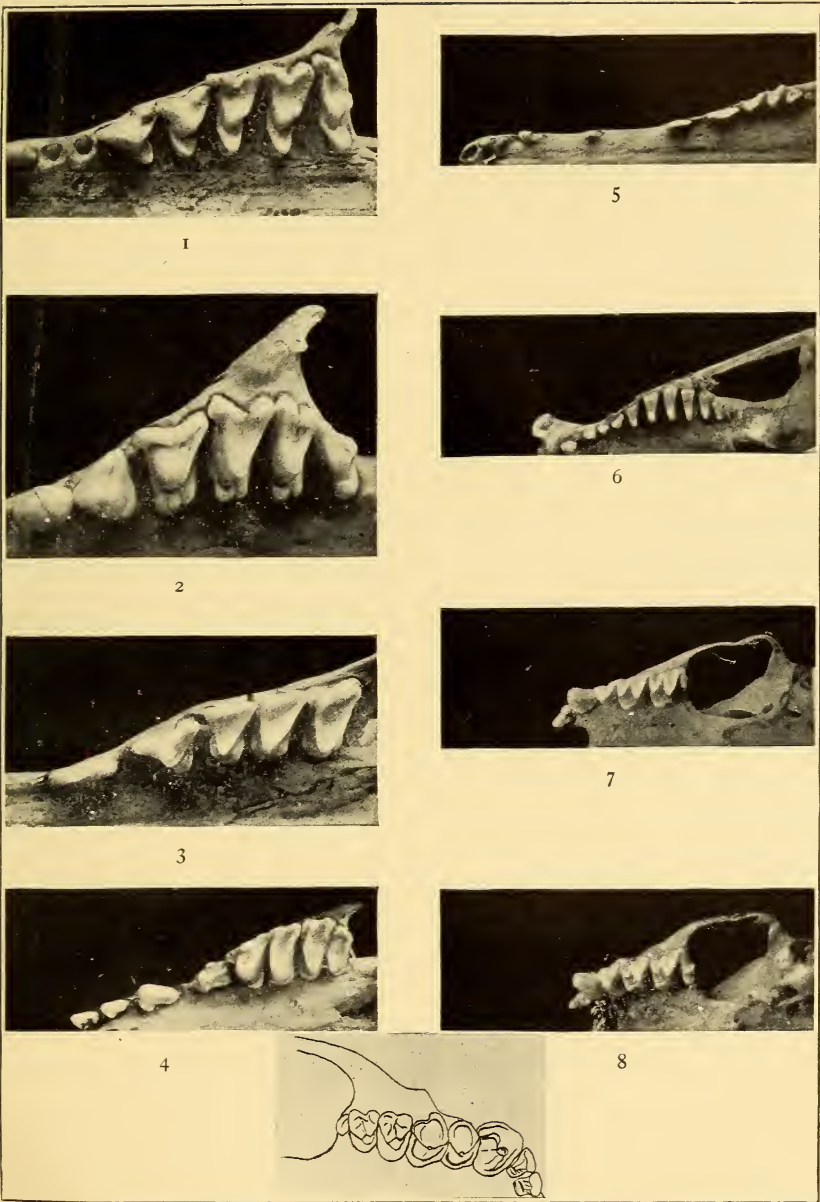
Viewed from the nomenclature standpoint, therefore, the convenient names proposed by Osborn have come to assume an individuality which conveys a far more definite meaning than any purely descriptive terms, be they of relative position or supposed homologies. Moreover, they have the valuable advantages of clearness and brevity in description. On these grounds, in the opinion of the present writer, and for the added reason that great confusion would inevitably result from any change in a terminology that has found its way into so many publications, Osborn's nomenclature should be retained as originally proposed. Thus the term "protocone" always means the main antero-internal cusp of a normal upper molariform tooth, whether that element is regarded as the original primary cusp or otherwise.

The objection that the terms are not universally applicable is scarcely worthy of consideration since they are widely applicable to the great majority of mammalian molar types, without in the least interfering with the use of terms descriptive of "relative position only," which may be used in any cases where Osborn's terms do not apply.

EXPLANATION OF PLATE IV.

(All figures except fig. 9, three times natural size.)

- FIG. 1. *Potamogale*—left upper jaw (No. 124327 U. S. N. M.); habitat, Africa.
FIG. 2. *Solenodon*—left upper jaw (No. 2230, U. S. N. M.); habitat, Cuba.
FIG. 3. *Centetes*—left upper jaw (No. 63316 U. S. N. M.); habitat, Madagascar.
FIG. 4. *Ericulus*—left upper jaw (No. 122488 U. S. N. M.); habitat, Madagascar.
FIG. 5. *Hemicentetes*—left upper jaw (No. 63319 U. S. N. M.); habitat, Africa.
FIG. 6. *Chrysochloris*—left upper jaw (No. 61686 U. S. N. M.); habitat, Africa.
FIG. 7. *Vespertilio fuscus*—left upper jaw (No. 62736 U. S. N. M.); habitat, Washington, D. C.
FIG. 8. *Scotoophilus kuhli*—left upper jaw (No. 113463 U. S. N. M.); habitat, Philippines.
FIG. 9. *Harpiocephalus*—right upper jaw. (Outline drawing taken from a plate prepared in 1880 by Wilhelm Peters for a monograph of the bats. This monograph was never published.)



CHEEK TEETH OF LIVING INSECTIVORES AND BATS

EXPLANATION OF PLATE V.

- FIGS. 1 and 1a. *Triconodon* ? *bisulcus* Marsh (Atlantosaurus beds), left upper molars, m^2 and m^3 , crown and external views. Six times natural size (No. 2698 U. S. N. M.).
- FIGS. 2, 2a and 2b. *Dryolestes* sp. (Atlantosaurus beds), left upper molars; crown, external, and posterior views. Seven times natural size (No. 2845 U. S. N. M.).
- FIG. 3. *Dryolestes*, first right upper molar, m^1 ; crown view. Eight times natural size (No. 2839 U. S. N. M.).
- FIGS. 4 and 4a. *Dicrocynodon* sp. (Atlantosaurus beds), left upper molars; crown and external views. Six times natural size (No. 2715 U. S. N. M.).
- FIGS. 5, 5a, 5b and 5c. *Paurodon* sp. (Atlantosaurus beds), right lower molar, m_2 , crown, external, internal and posterior views. Eight times natural size (No. 2733 U. S. N. M.).
- FIGS. 6, 6a, 6b and 6c. ? *Pedionomys* sp. (Laramie beds), left upper molar; crown, external, posterior, and anterior views. Eight times natural size (No. 5062 U. S. N. M.).
- FIGS. 7, 7a and 7b. Gen. et sp. indt. (Laramie beds), left upper molar; crown, external and anterior views. Eight times natural size (No. 5076 U. S. N. M.).



1



1a



2



2a



2b



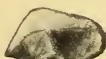
4



4a



3



5



5a



5b



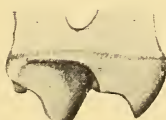
5c



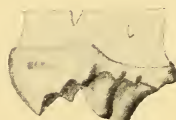
6



6a



6b



6c



7



7a



7b





